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FLOWER INDUCTION AND STIMULATION IN WESTERN WHITE PINE

by

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and
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Burton V. Barnes and R. T. Bingham[1]

INTRODUCTION

Tree improvement programs are necessarily concerned with flower induction. Both the time and cost involved in producing and tending progenies and the need to get graft or seedling orchards into production compel research efforts in flower induction. Empirical studies are helpful in establishing effective kinds and levels of treatments devised long ago by horticulturists and plant breeders to induce or stimulate flowering.

LITERATURE REVIEW

The literature on the nature of flowering and its control reflects the increasing interest of plant physiologists, biochemists, agronomists, horticulturists, and foresters. Matthews (1963), Nienstaedt (1961), and Richardson (1962) have reviewed the flower induction literature applicable to woody plants. The brief review below summarizes literature pertinent to the experiments described later in this report.

All plants pass through a vegetative stage before they reach the stage of ripeness-to-flower (Bonner and Galston 1952). Therefore, one approach for the scientist is to explain the basis of the transition from vegetative to flowering stage and discover means to effect this shift as quickly as possible. A second and equally important research task is stimulating flower production once the ripeness-to-flower stage has been attained. First, let us examine our knowledge of the vegetative and flowering stages in woody species and then consider (1) the transition from one stage to the other and (2) flower stimulation once the ripeness-to-flower stage has been reached.

In many woody plants the vegetative or juvenile stage (or stages) is distinguishable from the ripeness-to-flower or adult stage. The lower parts of a tree typically may remain in the juvenile stage after the upper parts have attained the adult stage. The difference between the two stages has been demonstrated by differences in flowering behavior, flushing, rooting capacity, and various vegetative characteristics (leaf shape and size, leaf abscission, leaf color, presence or absence of thorns, etc.). Many experiments have shown that lack of flowering is characteristic of the juvenile stage in woody plants (Schaffalitsky de Muckadell 1959). Both the genetic constitution of the plant and the environment may affect the duration of the juvenile stage (Mergen 1961; Nienstaedt 1961; Schaffalitsky de Muckadell 1959). Possibly, environmental changes can more effectively promote flowering the nearer the plant is to the adult stage--or some environmental conditions (such as nutritional status) can prolong the juvenile period.

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[1] Research forester and plant pathologist, respectively, U.S. Forest Service, Intermountain Forest and Range Experiment Station, Moscow, Idaho.

Robbins (1957) has given a good working hypothesis of the nature of the juvenile phase:

> ". . . I suggest as a working hypothesis that juvenility is an instable metabolic state which exists in the meristem and which proceeds through a series of steps to a relatively stable metabolic state characteristic of the adult meristem. The change from unstable to stable may be associated with the loss in ability to synthesize physiologically important chemical substances and/or the development of the ability to synthesize others."

Thus, a chemical substance, such as the flowering hormone (Bonner and Liverman 1953; Bonner 1959) probably regulates flowering once the adult stage has been attained.

Through experiments with Betula, Wareing (1959) found that the "attainment of a certain absolute size is the primary factor determining the transition to the adult condition . . . ." Büsgen and Münch (1929), Langner (1951), and Matthews (1955) also have observed that, in general, vigorous, healthy trees are the first to bear flowers. Wareing also postulates that in some species "the attainment of the flowering condition depends upon a certain degree of aging of the shoot-systems." The terms "maturation" and "aging" were put forth by Wareing to distinguish between the transition from the juvenile to the adult stage (maturation) and the loss of meristematic vigor as the tree develops (aging). Whether the physiological processes governing these phenomena are clearly different seems still open to question.

Mergen (1961, 1962) successfully induced male and female strobili on white pine hybrids (Pinus griffithii McClelland X Pinus strobus L.) less than 2 years old by combined high temperature and humidity and liquid fertilizer treatment. Unless this phenomenon is solely associated with interspecific hybridization, it demonstrates that by manipulation of the environment, flowering can be induced on trees apparently in the juvenile stage. Whether the flowering condition has been permanently fixed without annual treatment is yet to be determined.

Once the ripeness-to-flower stage is attained, flowering may commence immediately and automatically in some plants. For other plants, however, favorable environmental conditions are necessary for the onset of flowering. The two factors typically involved are relative day-length and temperature. In some plants photoperiodic treatment can permanently induce flowering. Phytochrome, the substance responsible for triggering the production of the flowering hormone, recently has been detected and extracted (Borthwick and Hendricks 1960). Phytochrome is a blue or bluish-green protein existing in two forms interconvertible by light (ibid.), and is known to control numerous biological phenomena, e.g., seed germination, pigment formation, elongation, etc. (Hendricks 1959). Photoperiodic treatment induces a chain reaction whereby a floral hormone is produced in the leaves and thence translocated to the buds where flower bud differentiation commences.

Woody species are thought to be day-neutral plants (Mirov 1956; Wareing 1959), i.e., plants whose flowering is controlled by factors other than relative length of day and night. Though day-length apparently has little effect upon flowering in forest tree species, it cannot be entirely disregarded. Larson (1961) introduced evidence to show that synchronization of climatic conditions and relative day-length with bud development may exert an influence upon flowering behavior.

Foresters have had varied success with cultural treatments, grafting, girdling, root pruning, strangulation, etc., to induce or stimulate flowering. Zobel et al. (1958) reviewed this literature and concluded that, although numerous methods have promoted or stimulated flowering in given instances, several were probably too injurious to use in seed orchards. Further, they believe the most satisfactory and safest method to be fertilization, together with moderate root pruning.

Soil fertility, fertilizers, and nutritional requirements of crop plants have been reviewed in detail by Åslander (1958) and Tisdale and Nelson (1956). Forest fertilization literature has been compiled by White and Leaf (1958), the relationship of mineral nutrition and growth of forest trees described by Leyton (1958a, 1958b), and the appropriate use of fertilizers in forest nurseries and stands summarized by Wilde (1958, 1961). Studies of fertilization in relation to soil deficiencies and plant deficiencies have received considerable attention (Heiberg and White 1951; Stoate 1950; Stone 1953; Swan 1960, 1961).

DESCRIPTION AND RESULTS OF THE EXPERIMENTS

The chief purpose of the experiments described below was to discover means of inducing strobilus[2] formation in young seedlings and grafts of western white pine. Experiment 1 was an attempt to induce flowering of seedling scions by grafting them into the crown of (a) trees of fruiting age and (b) young trees from 10 to 15 years old approaching fruiting age. Experiment 2 was similar to 1(b)--grafting seedling scions into 15 trees about 12 years old at each of two locations in northern Idaho and at two locations in western Washington (where many 7- to 10-year-old trees were found bearing female strobili). The effect of fertilizer, water, and cultivation upon strobilus production on 10-year-old wild trees was investigated (experiment 3). In experiment 4, cone bearing trees about 30 years old were fertilized in an attempt to stimulate strobilus production. All experiments were established in 1955 with the exception of experiment 2 (established in 1956), and all tests were observed annually through 1960.

EXPERIMENT 1. TOP GRAFTING--IDAHO EXPERIMENTS

At each of three locations in the St. Joe National Forest (Clarkia Peak, Butterfield Meadows, and Sheep Creek) 5-year-old seedling scions were grafted into the tops of two trees of fruiting age (average age 28 years) and five trees about 12 to 15 years old. Grafting, using the approach graft technique with budding bands was accomplished during mid-June of 1955. The seedling, still in its pot, was tied into the stock tree. The graft union was covered with a small handful of moist peat moss and wrapped with a small piece of vinyl film. Five seedlings from the same nursery lot as the scions were planted in the open near each stock tree to serve as controls.

Of 76 grafts attempted on the six fruiting-age trees, 57 percent survived the first year and 51 percent were alive in July 1960. Although all stock trees were observed flowering annually, no flowering was observed on the seedling scions. Of the 30 control seedlings planted, 29 were alive in 1960; in 1960 one male strobilus was discovered.

One hundred and nine grafts were attempted in the 15 young trees; 28 percent survived the first year, and 27 percent were alive in July 1960. No flowering was observed during the period 1956-1960. Of the 45 control seedlings planted (3 near each stock tree) 44 percent were alive in 1960, and no flowering had been observed.

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[2] The term strobilus is used to designate the juvenile female reproductive structure (before pollination); the term cone is used to designate all later stages (overwintering, maturing) of the same structure.

Besides the grafts in the two trees of fruiting age at each of the three sites, 4-year-old scions were grafted into the top of one heavily fruiting tree near Butterfield Meadows in 1951 as a preliminary test. One scion bore eight female strobili in 1958 (scion age 11 years), three in 1959, and three in 1960.

EXPERIMENT 2. TOP GRAFTING--IDAHO-WASHINGTON EXPERIMENTS

Two 6-year-old seedling scions were grafted by the approach method into the top of each of 15 young pines at each of two sites in northern Idaho and western Washington in May 1956. Average age of Idaho trees was 12 years; average age of Washington trees was 14 years. Two seedlings from the same nursery lot as the scion material were planted near each stock tree. Grafted pines and planted control seedlings were released as necessary to provide opportunity for growth and flowering.

In spite of animal and vandal damage, 85 percent grafting success was achieved at the Idaho plots and 93 percent at the west coast plots 1 year after grafting. In 1960 (scion age 10 years), 43 percent of the Idaho grafts were alive, but no strobili were observed on scions during the 4-year period. Two stock trees flowered in 1959. No strobili were observed on the planted seedlings.

Both graft survival (72 percent) and flowering were greater at the west coast plots. Seven stock trees and six scions flowered during the period 1956-1960. Grafted scions produced five female strobili, all of which aborted; 17 male strobili were produced.

EXPERIMENT 3. CULTIVATING, WATERING, FERTILIZING YOUNG TREES

At each of three locations in northern Idaho, five pairs of trees (average age 11 years) were selected for uniformity in age, vigor, and growing space. All trees were released from competing trees and shrubs. One tree of each pair received annual water, cultivation, and fertilizer treatments; the other tree received no treatment. A 14-14-14 nitrogen-phosphorus-potassium fertilizer was spread around all treated trees at the rate of 1 pound per 2 feet of tree height, or at a rate of approximately 370 pounds each of N, P_2O_5 (161 pounds of elemental P), and K_2O (307 pounds of elemental K) per acre. Treated trees were cultivated annually at the time of fertilizer application in May. Trees were watered one to three times per summer, depending on summer moisture conditions.

Of the 15 treated trees 11 were alive in 1960. Mortality was due to cultivation (2 trees), blister rust canker (1 tree) and bulldozing (1 tree). Three of the 11 trees produced 13 female strobili and 21 clusters of male strobili (table 1). All 15 untreated trees survived and one tree produced 24 female strobili, but no male strobili (table 1). Most of the female strobili (65 percent) were produced in 1958--a bumper year for strobilus production. This peak of production also coincided with the most watering in a previous summer, and the earliest application of fertilizer (April 30 vs. ca. May 27 in other years).

The average total height of treated and untreated trees in 1955 was identical (5.5 feet); in 1960, untreated trees were slightly taller than treated trees (14.8 feet vs. 14.6 feet). Treated trees have failed to grow faster than untreated trees; furthermore, of the four treated trees, two died as a direct effect of cultivation injury.

Because of the expense of irrigation treatment, the frequency of application was held to a minimum. More liberal application of this treatment might cause greater effects.

Table 1.--Strobilus production by young western white pine trees in experiment 3

Location		Trees in 1955	Trees in 1960	Strobilus production											
				1956		1957		1958		1959		1960		Total	
				♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Keeler Creek	(Treated[1]	5	4	0	0	0	0	1	0	0	0	0	0	1	0
	(Untreated	5	5	0	0	0	0	0	0	0	0	0	0	0	0
Butterfield Meadows	(Treated	5	4	0	0	0	[2]4	8	2	0	15	4	0	[3]12	[4]21
	(Untreated	5	5	0	0	4	0	16	0	4	0	0	0	[5]24	0
Sheep Creek	(Treated	5	3	0	0	0	0	0	0	0	0	0	0	0	0
	(Untreated	5	5	0	0	0	0	0	0	0	0	0	0	0	0

[1] Trees receiving cultivation, fertilizer, and water treatments annually.

[2] Number of clusters of male strobili.

[3] ♀ Strobili produced by three trees.

[4] ♂ Strobili produced by two trees.

[5] ♀ Strobili produced by one tree.

EXPERIMENT 4. STIMULATING STROBILUS PRODUCTION IN FRUITING-AGE TREES

Three groups of four fruiting-age trees (average age 28 years) in the St. Joe National Forest near Elk River, Idaho, were selected to test the effect of fertilizer levels on strobilus and cone production. Initially the four fertilizer treatments were 0, 5, 10, and 15 pounds of a nitrogen, phosphorus, and potassium mix per tree. Each treatment was given to three trees--one randomly selected tree in each of the three groups. In late May 1956, fertilizer was spread around each tree on an area approximately equal to the crown projection. Although for a given treatment the same amount of fertilizer was given to each tree, the effective amount per acre would vary with the crown projection area of the tree. In general, the rate per tree in pounds of fertilizer was (1) 5--approximately 100 N, P_2O_5 (44 of elemental P) and K_2O (83 of elemental K) per acre, (2) 10--200 per acre, and (3) 15--300 per acre. Fertilizer application was initially scheduled for 1956 only, but because no increase in strobilus production was noted in 1956 or 1957, subsequent applications--doubling the original treatment levels--were made in the spring of 1958 and of 1959. Early in mid-July of each year during the period 1956 through 1960, strobili and cones were counted by climbing each tree and examining each branch.

The results show no obvious or general stimulating effect of fertilizer on strobilus production (table 2). Strobilus production was erratic. Neither the hypothesis that spring fertilization will stimulate strobilus production the same year nor the hypothesis that the increase will occur the following year satisfactorily explains these data. The total production for the 5-year period reveals no marked differences in the four treatments.

Table 2.--Strobilus production by fertilized and unfertilized western white pine trees, Butterfield Meadows, St. Joe National Forest, Idaho, experiment 4

Fertilizer treatment[1]	Number strobili produced[2]						
	1956[3]	1957	1958[3]	1959[3]	1960	Total	Average per tree per year
No treatment	59	326	566	196	102	1249	83
5 (10) pounds	97	203	502	169	357	1328	88
10(20) pounds	30	400	289	244	133	1096	73
15(30) pounds	103	131	344	168	373	1119	75

[1] Initial treatments of fertilized trees were 5, 10, and 15 pounds in 1956; in 1958, treatments doubled to 10, 20, and 30 pounds.

[2] For each year the number of strobili is the sum of the strobili produced on three trees treated alike.

[3] Year of fertilizer application.

The great loss of cones due to insect infestation (Conophthorus monticolae Hopkins) is striking (table 3). Although the percent of uninfested cones for treated trees is somewhat greater than for untreated trees, too few trees were observed for a meaningful comparison. Insect damage was assessed only in the spring. The extent of damage occurring in the summer, caused by Dioryctria abietella (D.&S.) and Eucosma rescissoriana Heinrich, was not determined.

Table 3.--Uninfested cone production by fertilized and unfertilized western white pine trees, 1957-1960, Butterfield Meadows, St. Joe National Forest, Idaho, experiment 4

Fertilizer treatment[1]	Cone production[2]									
	1957		1958		1959		1960		Total	
	No.	Percent uninfested[3]	No.	Percent uninfested	No.	Percent uninfested	No.	Percent uninfested	No.	Percent uninfested
No treatment	59	12	208	4	442	1	184	1	893	3
5 (10) pounds	96	73	139	9	462	2	118	3	815	11
10(20) pounds	29	17	171	5	322	1	210	1	732	3
15(30) pounds	103	67	75	4	302	3	87	9	567	16

[1] Initial treatments of fertilized trees were 5, 10, and 15 pounds in 1956; in 1958, treatments doubled to 10, 20, and 30 pounds.

[2] Number of immature cones counted annually in July on three trees treated alike.

[3] Percent of total cones free of Conophthorus monticolae at time of cone count in July each year.

DISCUSSION

Not one of the methods attempted was successful in markedly inducing or stimulating strobilus production of western white pine during the test period. In Idaho, top grafting was successful in only one instance (7 years after grafting at scion age 11), where a single, heavily fruiting stock tree was selected. Instances of precocious flowering when juvenile scions were grafted into the tops of heavily fruiting trees have been reported by Mirov (1951) with pine and Kemmer (1953) with apple. Most of the evidence, including these trials with western white pine, indicates that flowering is not markedly hastened by grafting juvenile scions onto adult stocks (Schaffalitzky de Muckadell 1959; Mergen 1962). Apparently precocious flowering can only occur when the shock or nutritional change is great enough, or when a highly labile genotype is involved. Top grafting in western white pine is probably not a practical or feasible way to effect the change from the juvenile to adult condition.

Cultivating, watering, and fertilizing of young, wild trees did not substantially increase flowering although a slight increase for treated trees was noted at one location. Although more intensive application or different timing of these treatments might have increased flowering somewhat, it appears that no overall and rapid change from the juvenile to adult stage can be achieved in wild trees.

Thus far, it appears that Wareing's hypothesis of plant size as an important criteria for flowering probably offers the best possibility for achieving early and abundant flowering. Attainment of a certain absolute size or degree of complexity possibly may be the best practical way to achieve early flowering for western white pine grafts or seedlings. In seed orchard management, precocious flowering is only initially important, thereafter the quantity and quality of production will be more highly prized. Cultivation, fertilization, and watering is known to markedly increase growth and complexity of young, seedling western white pine (U.S. Department Agriculture, Forest Service 1961). Large trees should have the physical capacity to produce more abundantly than much smaller trees which conceivably might be forced into early production by mechanical mutilation.

The liquid fertilizer and high temperature and humidity shock treatment used successfully by Mergen[3] with Pinus strobus L. and Pinus griffithii McClelland X P. strobus is also promising, particularly if the treatment effects a permanent change from nonflowering to flowering stage.

Late May through early June fertilizer application did not increase strobilus production of fruiting-age pines. Fertilizer treatment is known to stimulate flowering of reproductively mature trees in a number of woody species (Allen 1953; B.C. Forest Service 1960; Hausser 1960; Hoekstra and Mergen 1957; Mayer-Krapoll 1959; Steinbrenner et al. 1960; Stoate et al. 1961; Wenger 1953), and we know it can promote flowering in western white pine.[4] Thus, failure in this test may be due to several reasons, e.g., (1) high nutrient status of the trees, (2) improper time, amount, or method of fertilizer application, and (3) large differences between the trees (site, surrounding density, inherent fruitfulness, etc.). Wilde (1961) stresses clearly that indiscriminate application of fertilizer will not always stimulate flowering.

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[3] Mergen (1961, 1962), and personal communication April 10, 1962, from Francois Mergen, Associate Professor of Forest Genetics, School of Forestry, Yale University.

[4] Replicated experiments in a western white pine seed production area showed that both nitrogen and N-P-K fertilizer applications at the rate of 300 pounds per acre significantly increased strobilus production in 40-year-old trees.

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Barnes, Burton V., and R. T. Bingham
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Strobilus induction or stimulation of western white pine trees in northern Idaho was attempted in four tests employing top grafting and various combinations of cultural treatments. No marked increase in flowering was observed in any test. Western Washington top grafting experiments proved more successful than similar tests in northern Idaho but all female strobili produced have aborted.

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